A COMPARATIVE STUDY OF EPIGYNY IN CERTAIN MONOCOTYLEDONS AND DICOTYLEDONS*

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It is not the purpose of this study to give the complete details of the organography of the different flowers, which have been chosen for this comparison but the steps in the development of the floral organs have been given in sufficient detail to show the development of the inferior ovary. From these a comparison of epigyny in the two great divisions of the flowing plants has been made. Very little work has been done on this special phase of the subject, although different writers have their own explanation for the manner in which epigyny is produced.

Martin (6) in 1892 wrote, "The real origin and behavior of the floral organs in their younger stages of development as correlated with the inferior ovary has attracted but little attention, and therefore, no definite statement can be made as to the true relationship existing between the floral organs in their embryonic condition". In the same paper, in speaking of the tubular mass of tissue, he wrote, "In which there is a complete fusion of the parts until liberated", and a theory was proposed "that all the floral organs are coalesced in their initial state in the annular wall, and each appears as the upper parts are liberated".

Gray (5) wrote, "Where the adnation is complete to the top of the ovary and none beyond it".

Goebel (3) in 1887 defined an epigynous flower in this manner, "The walls of the ovary are formed from the torus itself, which is hollowed out into the shape of a cup, or even a long tube, while the carpels which form the entire wall of the free superior ovary, spring like the perianth and androecium from the margin of the hollow torus and only close its cavity above, being there prolonged into the style and bearing the stigma. The inferior ovary is formed by the terminal growth being retarded and by the outer rim growing upward. The placentae may be regarded as the margins of the carpels running down the inner surface of the ovary wall".

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In his Organography of Plants, published in 1901, Goebel (4) said in contradiction to what he had said in his book, published in 1887, "On account of deficient historical investigation, the view was formerly advanced, that the ovary of the epigynous flower is formed from the cup-like flower axis, and the carpellary leaves only produce the style and stigma. Comparative morphology has rightly contradicted this interpretation, which is still found in many books. As the history of the development shows, the carpels share in the formation of the ovarian cavity, and the ovules have no other origin than in the superior ovary.

"In all inferior ovaries, the vegetative point becomes at an early period more or less concavely hollowed out, and the leaf structures of the flower arise, partly from the margins, and partly from the inner surface of the depression. Whether one describes the marginal part of the flower axis as a 'congenital concrescence' of the different leaf whorls of the flower is an arbitrary matter, because the flower axis ends its active existence with the bringing forth of the leaf structures of the flower. The earlier the flower axis assumes the cup-like form, the more will we in general ascribe its character to the flower axis. The later this form is assumed the more will its features approach the more primitive condition as we find it in hypogynous flowers".

Wylie (8) in 1904 worked out the morphology of *Elodea canadensis*. In this study, he showed how epigynous flowers have developed in this primitive type of monocotyledon.

Coulter (1) in 1883 investigated the dandelion flower, giving as his purpose an investigation of the development of the inferior ovary. He said, "The inference is that all four of the floral organs are blended together in the primitive ring, which rises from the original obconical mass, that they are essentially hypogynous and that their separate appearance is a freeing of their upper extremities. It was attempted in vain to detect in the primitive ring or later in the wall of the ovary any evidence of the blending of two or more distinct parts. No such indication could be found, and the inference that all four floral parts are represented in the wall of the inferior ovary rests, not so much upon the structure of the wall, as upon the order of the succession in the appearance of the floral parts".

He believes the theory, that the primitive ring belongs to the receptacle, is not tenable for two reasons: (1) "the late appearance of the calyx"; (2) the fact that the corolla lobes appear with the ring and not after it, indicating that the ring belongs to the floral organs. "The inferior ovary is produced by an arrest of the development of the floral axis the rising in a peripheral ring of the floral organs and a gradual arching over of the carpellary leaves".

Merrell (7) in his paper on Silphium said, "The outline of the receptacle soon became angular by the upward growth of the marginal ring, which is the beginning of the corolla tube".

Six species of Monocotyledons and nine species of Dicotyledons, representing twelve different families, have been included in this comparative study.

The different species are named below under their respective groups:

1. Monocotyledons: *Sisyrinchium augustifolium; Gladiolus gandavensis; Iris germanica; Freesia refracta, Var alba; Musa sapientum;* and *Canna indica.*
2. Dicotyledons: *Malus ioensis, Ribes aureum, Fuchsia speciosa, Citrullus vulgaris, Sanicula canadensis, Galium aparine, Sambucus canadensis, Valeriana officinalis* and *Helianthus annuus.*

Monocotyledons. Plates XXVIII-XXXI

Sisyrinchium angustifolium. Plate XXVIII

The flowers are produced in clusters, developing in centripetal order. The buds begin as protuberances of meristematic tissue, which appear slightly triangular in cross section, due to the arrangement of the flowers in the cluster. Soon three lobes, the beginning of the stamens, grow up from the rim of the receptacle, which has become flattened (Plate XXVIII, Fig. 2). The lobes of the perianth soon appear at the sides of the mass (Fig. 3). At about the same time, the tissue just below the origin of the perianth and the stamens begins to elongate, forming a tubular ring about a shallow cavity in the center (Figs. 4, 5 and 7). The three lobes, which are to form the carpels, soon grow out from the inner rim of the tubular cavity (Figs. 5 and 6). A mass of tissue soon roofs over the central cavity, and a continuation of the three lobes upwards forms the style branches (Fig. 12). From three sides of the cavity, tissue begins to grow towards the center (Fig. 8). The fusion of these three outgrowths divides the ovary into three parts (Figs. 10 and 11). The tissue at the point of origin of the sepals and the petals grows *en masse,* so that the sepals and petals are joined together for a short distance, forming a tubular ring.

Gladiolus gandavensis. Plates XXVIII and XXIX

The earliest stages in the development of the flower of the Gladiolus were not found, but stages showing the growth of the tissue forming the tubular rim and the central cavity are shown in Plate XXVIII, Fig. 13. The perianth and stamen lobes have appeared. Further development is similar to Sisyrinchium. The figures show the origin of the parts and the final development of the inferior ovary. The order of the succession of the floral leaves is sepals, petals, stamens and pistils.

Iris germanica. Plate XXIX

The development of the flower of the Iris is almost the same as that of Sisyrinchium angustifolium, differing in the order of the succession in the development of the floral leaves. In the Iris, the order is perianth, stamens, and carpels (Figs. 2, 3 and 4). The petals and stamens appear almost at the same time, so nearly so, that it is difficult to determine which lobes really appear first. In Sisyrinchium, the stamen lobes grow out first (Plate XXVIII, Fig. 2) and the lobes of the perianth grow out at the sides, as described under Sisyrinchium and shown in (Plate XXVIII, Fig. 3.)

Freesia refracta. Plates XXIX and XXX

The flowers are produced on two sides of an elongated axis, each flower subtended by a bract. The flower begins as a protuberance from the side of the flower axis. This undifferentiated mass of cells soon flattens and broadens, and distinct lobes appear, the sepals (Fig. 7). Inside the whorl of sepals, the stamens appear (Fig. 8). At this time, the tissue below the lobes begins to elongate, forming a tubular ring with a shallow cavity in the center (Fig. 9). The lobes of the carpels appear (Fig. 1 and 2, Plate XXX). There is further elongation of the tissue just below the point of origin of the floral organs. The three carpel lobes grow out into the central cavity, and, growing upward and toward the center, cover the cavity. An upward extension of the three masses forms the three style branches, which appear as three lobes only at the top (Fig. 3).

Musa sapientum. Plate XXX

The method of origin and early development of Musa sapientum is like the Iris, Freesia and Gladiolus. The later development shows a zonal development of the tissue near the bases of the sepals and petals, so that the sepals and two of the petals are joined together nearly to their tips. The other petal remains free.

Canna indica. Plates XXX and XXXI

The flower begins as an outgrowth which broadens; the sepals grow out from the top of this undifferentiated mass (Fig. 11, Plate XXX), and just inside of these lobes, other masses grow out. and very soon separate into two parts (Plate XXXI, Fig. 1). The inner whorl forms the four staminoidia and the one fertile stamen, and the other whorl the petals. The tissue at the base of these lobes now elongates in the peripherial portion leaving a hollow central cup (Figs. 2 and 3). Further devolpment resembles Sisyrinchium, differing in the form of the style. The tissue at the upper portion of the central cavity grows up into a somewhat flattened mass forming the style (Figs. 4 and 5).

Wylie (8) found the development of the primitive, Monocotyledon, *Elodea canadensis,* quite like that given above for the higher Monocotyledons. Buds begin as protuberances, apex of receptacle flattens and broadens, a mass of tissue grows up leaving a tri-radiate slit down the center. The order in Elodea is sepals, three sterile stamens, three stigmatic lobes, and finally the petals.

In the Monocotyledons described above the tri-radiate slit did not form until after a circular cavity formed and three masses of tissue grew out into this cavity.

Dicotyledons. Plates XXXI-XXXV

Malus ioensis. Plates XXXI and XXXV

Material was not collected early enough to show the first stages in the development of the flower of the Malus, but early stages to show the development of the inferior ovary were found. The floral organs, sepals, petals and stamens are shown in Plate XXXI, Fig 6. At the time that the lobes of the floral organs appear, there is an upward growth of the outer rim of the receptacle, leaving a shallow, broad, central cavity (Fig. 7). The carpel lobes grow out from the bottom of this shallow cavity (Fig. 8). The elongation of the rim of this cup produces the wall of the inferior ovary (Fig. 9). Very soon after the appearance of the lobes of the carpels, a cross section of the ovary shows five masses of tissue growing in toward the center (Fig. 10).

Ribes aureum. Plate XXXII

The order of the development of the floral organs of Ribes is similar to that of Malus. The elongation of the cylindrical mass of tissues leaves a narrow slit (Fig. 3), from the sides of which, two protuberances grow out, forming two opposite lateral placentae (Figs. 4, 5 and 7). Two lobes of the style form with only one cavity in the ovary. The cross section shows two bundles, one for each carpel (Fig. 7 d).

Fuchsia speciosa. Plates XXXII and XXXIII

The flowers are solitary in the axils of opposite leaves. The flower buds begin as hemispherical masses of undifferentiated tissue (Plate XXXII, Fig. 8a). The receptacle flattens, and the four lobes of the sepals appear on the peripheral portion. This outer portion elongates, forming a shallow cup-shaped cavity in the center (Figs. 9 and 10). The petals and stamens grow out from the inner surface of this cup, near the bottom (Fig. 11).

The zonal development continues. The cup-like cavity elongates. Just below the stamens, the four lobes of the carpels appear (Fig. 12). An upward prolongation of these lobes forms the style branches and roofs over the central cavity (Fig. 13). The four cavities of the ovary are formed by four masses of tissue growing toward the center and fusing. (Plate XXXIII, Figs. 1, 2 and 3).

Citrullus vulgaris. Plate XXXIII

The origin and development of the floral organs of the flowers of Citrullus are very similar to those of Fuchsia, except for the number of parts. There are the five sepal lobes (Fig. 6), petals (Fig. 7) and stamens (Fig. 8). As in the other Dicotyledons, there is the hollow cavity in the center (Fig. 9). The sides of the cup elongate to form the inferior ovary (Fig. 11).

Sanicula canadensis. Plates XXXIII and XXXIV

What has been said about the Fuchsia is also true, in part, for Sanicula. From the flattened receptacle the five lobes of the sepals grow out (Fig. 13). The petals appear just inside but alternate with the sepals (Fig. 13). At the point of origin of these parts there is the zonal elongation, so that the sepals and petals are adnate a short distance above the ovary. After the cavity of the ovary is formed, a two-lobed mass of tissue grows up from the bottom of the cavity (Fig. 15). The base of this tissue elongates carrying the lobes upward, until they meet the tissue, which roofs over the cavity of the ovary Plate XXXIV (Figs. 1 and 2).

Galium aparine. Plate XXXIV

The petals are the first of the floral organs to appear in Galium (Fig. 4). The sepals are late in appearing, and then do not develop very far (Fig. 5). Just below the stamens the stigmatic lobes appear and between these a convex mass grows out from the bottom of the cavity. This mass soon becomes two-lobed (Fig. 6), enlarges (Fig. 7), and develops two sporangia with their integuments (Fig. 8). With the appearance of the stigmatic lobes and the sporangia, there is an elongation of the tissue at the base of the sporangia. This upward growth and a downward growth from the roof tissue divides the central cavity into two separate locules (Figs. 9 and 10).

Sambucus canadensis. Plate XXXIV

The origin of the floral organs is the same as the others described. The sepals grow out from the edge of the flattened mass of tissue (Fig. 11). The petal lobes appear (Fig. 12) while the receptacle is still flat (Fig. 13). The sepals elongate and enclose the other parts. Figure 14 shows the appearance of the stamens. The central cavity flattens out, so that it becomes broad and shallow (Fig. 15). The carpel lobes appear as outgrowths from the bottom of the cavity (Fig. 16). This upward growth coalesces with four lobes growing in from the inner surface of the cavity. Tissue grows down from above and meets the upward growing tissue (Figs. 1 and 2, Plate XXXV).

Valeriana officinalis. Plate XXXV

The five lobes of the petals appear at the edge of the flattened receptacle (Fig. 4). The lobes on one side of the flower grow more rapidly than the others, forming a slightly zygomorphic flower. A single stamen grows out (Figs. 6 and 7). At the same time, there is an upward growth of the tissue at the base of the petals and the stamens (Fig. 7). The sepals grow out from the outer surface of the tubular ring, and the carpel lobes form near the bottom part of the inner surface of this ring. There are then two rapid zonal elongations, one of the tissues growing up to form the ovarian cavity, and the other the tissue at the base of the sepals and stamen. The petals form a tube and the stamen is joined to the petal some distance above its point of origin.

Helianthus annuus. Plate XXXV

The details of the development of the flowers of Helianthus are essentially like those for Valeriana. The order of the succession of the parts is petals, stamens and carpels (Figs. 10-16). The sepals appear at about the same time as the carpels. There are the two zonal elongations; one forms the tubular corolla, and the other the wall of the inferior ovary.

Summary

In conclusion, some of the points observed in the study of the development of the inferior ovary in the above species of Monocotyledons and Dicotyledons are summed up in the following comparisons of the two groups:

1. The flower buds of all originate in the same manner by a portuberance of undifferentiated, meristematic tissue growing out from the flower axis. This mass flattens and broadens, and several whorls of lobes appear at the upper outer edge.

2. The order of the succession in the development of the floral parts is not the same for all the genera of the Monocotyledons, nor for all the Dicotyledons. The order, sepals, petals, stamens and carpels is found in all the Monocotyledons except Sisyrinchium. The same order is found in all the Dicotyledons, except Helianthus, Galium and Valeriana. In these the order is petals, stamens, sepals and carpels. In Sisyrinchium, so far as could be determined, the stamens appeared first.

3. In none of the cross sections could there be found any evidences that several floral parts had begun as separate parts and then joined together.

4. In both groups, there is evidence of adnation of parts, but this union of parts is formed by a zonal elongation of the tissue at the point of origin.

5. An examination of one similar stage of development, through the whole series of plants studied (the stage chosen was the one showing the appearance of carpels, Plate XXXVI), shows one difference between the Monocotyledons and Dicotyledons. In the Dicotyledons the lobes of the carpels grow out from the bottom of a very shallow cup, while in the Monocotyledons the carpel lobes push out from the sides of a slightly elongated cup.

6. After the appearance of the carpel lobes the annular rings in all elongate, forming the inferior ovary. In some cases, the tissues above the ovary also elongate, so that the stamens appear to branch out from the petals, and in others the petals and sepals are joined.

The differences of opinion as to the origin and development of epigyny seem to be based on the question, whether inferior ovaries are formed by a coalescence of all parts until they are liberated above, or whether the receptacle grows up in the form of a cup with the lobes of the sepals and petals coming from the rim. After making a careful study of the different plants described above, it seems that epigyny in both the Monocotyledons and the Dicotyledons develops in practically the same manner. This appears to be by a zonal elongation of the tissues just below the point of origin of the floral leaves. This elongation may begin at the appearance of the first lobes or it may not begin until the lobes of all the parts have appeared.

The origin and development is similar, with the one exception given under 5 above, whatever theory as to the nature of the wall of the ovary, is accepted, whether it has the character of the floral axis or the character of the floral leaves.

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EXPLANATION OF PLATES

The lettering for all the figures is the same:

se = sepals	pl = placenta
pe = petals	s = stamens
p = perianth	st = style and o = ovules

Plate XXVIII

Figs. 1-12 *Sisyrinchium angustifolium* (X 68.7).

Fig. 1. The young stem tip on the left, a, young flower bud; b, bract.

Fig. 2. Longisection of a young flower bud, showing the beginning of the lobes of the stamens.

Figs. 3, 4, 5, 6 and 9. Longisections thru the center of young flower buds, showing the origin and growth of the sepals, petals, carpels and ovary cavity.

Figs. 7, 8, 10, 11. X—sections of ovary, showing central cavity in Fig. 7; the development of placenta and ovules in Figs. 8, 10, and 11; Fig. 7 about same stage as Fig. 4; Fig. 10 same as Fig. 9 and Fig. 11 as Fig. 12.

Fig. 12. Longisection of an older bud, showing the inferior ovary.

Figs. 13-15. *Gladiolus gandavensis* (X 68.7).

Fig. 13. Longisection of flower bud, s, beginning of stamen; p, perianth; b, bract.

Fig. 14. Older stage of same.

Fig. 15. Shows the beginning of carpels, c.

Plate XXIX

Fig. 1. *Gladiolus gandavensis* (X 23.2) se, sepals; pe, petals; st, style.

Figs. 2-6. *Iris germanica*. Figs. 2, 3, 4 (X 68.7). Figs. 5 and 6 (X 38.7). All are longisections of young flowers, cut near center of bud.

Fig. 2. Young flower bud; p, perianth; b, bract.

Fig. 3. s, beginning of stamens.

Fig. 4. Further development; c, carpels.

Figs. 5 and 6. Later stages of same.

Figs. 7-10. *Freesia refracta* (X 68.7). Longisections of young flower buds. s, stamens; perianth; se, sepals. Figures numbered in order of the appearance of different parts.

Plate XXX

Figs. 1-3. *Freesia refracta.* Figs. 1 and 2 (X 68.7).
Figs. 1 and 2. Longisections of the same flower. Fig. 1 cut thru the center and Fig. 2 at one side of the center.
Fig. 3. (X 38.7). Longisection of an older flower.
Figs. 4-9. *Musa sapientum* (X 68.7).
Fig. 4. Young flower bud.
Fig. 5. Longisection of an older flower bud.
Figs. 6-9. Longisections, showing origin and growth of parts as lettered.
Figs. 10 and 11. *Canna indica* (X 68.7).
Fig. 10. Longisections of three flower buds, a; b, bracts.
Fig. 11. L-section of one older flower. s+pe, stamens and petals; se, sepals.

Plate XXXI

Figs. 1-5. *Canna indica.* Figs. 1-3 (X 68.7); Fig. 4 (X 19.3).
Figs. 1, 2, 3 and 4. L-sections, numbered in order of development of parts and lettered as above.
Fig. 5. Cross section of pistil (X 19.3). a, cut near top of style; b, near center; c, below b.
Figs. 6-10. *Malus ioensis* (X 31.2).
Figs. 6, 7, 8, 9. Longisections, showing the origin and development of the parts of the flower.
Fig. 10. Cross section of a young ovary. pl, placenta.

Plate XXXII

Fig. 1. *Malus ioensis* (X 18.7). Longisection of a flower, the inferior ovary well developed.
Figs. 2-7. *Ribes aureum.* Figs. 2-5 (X 68.7); Figs. 6 and 7 (X 31.2).
Figs. 2, 3 and 6. Longisection of young flower numbered in order of development.
Fig. 4. Cross section of the ovary of Fig. 3.
Fig. 5. X-section of an older stage.
Fig. 7. X-section of pistil, stage same as Fig. 6.
a, cut at dotted line "a"; c, on dotted line "c"; and b, cut between "a" and "b"; d, cut thru ovary, shows young ovules.
Figs. 8-13. *Fuchsia speciosa.* Figs. 8-10 (X 68.7). Figs. 11-13 (X 31.2).
Fig. 8. Longisection of young stem tip.
a, a, young flower buds on either side of stem tip.
Figs. 9 and 10. Development of sepals.
Figs. 11, 12 and 13. Appearance of sepals, petals, stamens, and carpels. Dotted lines in Fig. 12 show where petals will appear as slide is moved along.

Plate XXXIII

Figs. 1-4. *Fuchsia speciosa.*

Fig. 1. X-section of very young ovary (X 68.7). Same stage as Plate V, Fig. 10.

Fig. 2. X-section (X 31.2) of older ovary.

Fig. 3. X-section of ovary of Fig. 4. (X 15.5).

Fig. 4. L-section of an older flower. (X 15.5).

Figs. 5-11. *Citrullus vulgaris.* Figs. 5-10 (X 68.7); Fig. 11 (X 31.2).

Fig. 5. Beginning of flower bud.

Fig. 6. Sepal lobes appearing.

Figs. 7, 8, 9, 10 and 11. L-sections of young flowers, showing the beginnings and development of sepals, petals, stamens and pistils.

Figs. 12-15. *Sanicula canadensis* (X 68.7).

Fig. 12. Beginning of flower bud, a;

Fig. 13. Three flower buds in different stages of development.

Fig. 14. Carpels have appeared.

Fig. 15. Two ovules growing up into central cavity.

Plate XXXIV

Figs. 1 and 2. *Sanicula canadensis* (X 31.2). Longisections of flower, with inferior ovary and ovules.

Figs. 3-10. *Galium aparine.* Figs. 3-8 (X 68.7). Figs. 9 and 10 (X 31.2).

Fig. 3. Longisection of young flower. Receptacle flattened.

Fig. 4. L-section; sepals and petals appear.

Fig. 5. Same. Carpels and placenta forming.

Fig. 6. Placenta two-lobed.

Figs. 7 and 8. Further development of parts, with two ovules.

Fig. 9. X-section of ovary cut at "m" Fig. 8.

Fig. 10. Same cut below Fig. 9.

Figs. 11-17. *Sambucus canadensis.* (X 68.7).

Fig. 11. L-section of fl. bud; lobes of sepals.

Figs. 12 and 13. Beginning and growth of petals.

Fig. 14. Stamens appearing.

Fig. 15. Growth of parts shown in Fig. 14.

Fig. 16. L-section. Carpel lobes just beginning.

Fig. 17. Placenta growing out from central cavity.

Plate XXXV

Figs. 1 and 2. *Sambucus canadensis* (X 31.2).

Fig. 1. Longisection of fl; beginning of ovules.

Fig. 2. Further development of parts already begun.

Figs. 3-9. *Valeriana officinalis* (X 68.7).

Fig. 3. Longisection of two fl. buds.

Fig. 4. Two fl. buds showing different stages of development.

Fig. 5. L-sections; petals present.

Figs. 6 and 7. L—sections; carpels appearing and developing.

Fig. 8. Elongation of two regions, forming inferior ovary and corolla tube.

Fig. 9. Inferior ovary and ovules.

Figs. 10-16. *Helianthus annuus.* (X 68.7).

Fig. 10. Flower buds appearing on flattened receptacle.

Fig. 11. One flower. Lobes of petals appearing.

Figs. 12 and 13. Beginning of stamens and carpels.

Figs. 14 and 15. Further development of floral organs.

Fig. 16. L-section of inferior ovary, stamens adnate to petals.

Plate XXXVI

Figs. 1-14. (X 68.7). L-sections of similar stages in the development of the floral leaves of the Monocotyledons and the Dicotyledons.

Figs. 1-6. Monocotyledons.

1. *Sisyrinchium angustifolium.*
2. *Gladiolus gandavensis.*
3. *Freesia refracta.*
4. *Iris germanica.*
5. *Canna indica.*
6. *Musa sapientum.*

Figs. 7-15. Dicotyledons.

7. *Malus ioensis.*
8. *Ribes aureum.*
9. *Fuchsia speciosa.*
10. *Citrullus vulgare.*
11. *Sanicula canadensis.*
12. *Galium aparine.*
13. *Sambucus canadensis.*
14. *Valeriana officinalis.*
15. *Helianthus annuus.*